

Grain-dependent habitat selection in white-tailed deer

(Odocoileus virginianus)

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By:

Michel Paul Philippe Laforge

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Abstract

A fundamental problem in ecology is determining what factors affect the distribution of organisms across a landscape. Landscapes are by their nature heterogeneous and different habitat types confer different fitness benefits and costs to organisms that inhabit them. Ecologists are now aware of the importance of examining multiple spatial scales when designing studies quantifying animal resource selection. Scale of analysis has been shown to be important, since ecological pressures relating to the establishment of a home range differ from those relating to the use of resources within the home range. Most studies that examine multiple spatial scales examine the effect of modifying extent. Here, I examine the role of grain, an underappreciated component of scale, on our interpretation of habitat selection patterns and functional response.

The goal of this thesis was to examine how grain size affects the interpretation of animal resource selection and functional response across multiple habitats. The perceptual range of an individual is known to change with habitat, therefore I hypothesized that resource selection and functional response would be both grain- and habitat-dependent, and that resource selection functions computed using different grains for different resources would be more predictive than models computed using only a single grain.

I used GPS-collared white-tailed deer (*Odocoileus virginianus*) to quantify resource selection functions at various grains and used generalized linear mixed effects modelling and multi-model inference techniques to examine how resource selection patterns changed with spatial scale across habitat types. I used selection ratios to examine functional response across grains. Model coefficients changed with grain and the strength of selection varied by habitat type. Multi-grain resource selection functions had lower AIC values and better cross-validation

scores than single grain models. Functional response varied with scale and habitat type, displaying a unique relationship for each habitat. My results suggest that spatial memory and habitat-dependent perceptual range play an important role in resource selection. I conclude that the examination of multiple grains in the study of animal habitat selection and functional response represents a step forward in our ability to understand what drives the distribution and abundance of organisms.

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List of abbreviations and notations

AIC	Akaike's Information Criterion
$AICw_i$	Akaike weight
GIS	Geographic information system
GPS	Global positioning satellite
MCP	Minimum convex polygon
MRSF	Multi-grain resource selection function
RMNP	Riding Mountain National Park
RSF	Resource selection function
w_i	Selection ratio

Chapter 1: Introduction

1.1 Resource selection functions

Ecology can be defined as “the scientific study of the distribution and abundance of organisms” (Andrewartha 1961). Hence, ecology is fundamentally tied to the habitats that organisms inhabit. Landscapes are by their nature heterogeneous, which has consequences for species that use those landscapes. Heterogeneity is an important driver of many ecological processes (Hobbs 2003), as different habitat types convey different benefits and costs for different species, a relationship that also varies temporally. As such, by quantifying the conferred fitness benefits of various habitat types on a given species, ecologists are able to generate predictive models of habitat use and subsequently model the distribution of species.

A powerful method of quantifying habitat suitability and animal habitat use is the resource selection function (RSF, Manly et al. 2002). RSFs compare the attributes (covariates) of used resources with either unused or available resources, depending on study design (Thomas and Taylor 2006). In the context of RSF analyses, a resource is defined as a point on the landscape. The attributes of this resource can then be measured, examining habitat (land cover class at that point), distance to a feature of interest (road, stream, etc), or the proportion of habitat types in the surrounding area. The independent covariates in an RSF have the flexibility of being categorical (e.g., habitat/land cover type), continuous (e.g., distance to roads), binary (e.g., in protected area: yes or no), or proportional (e.g., percent forest cover; Boyce & McDonald 1999).

The typical approach to the statistical analysis of RSFs is via a binomial generalized linear regression (Boyce et al. 2002). The result is a function that is proportional to the probability of use of a resource unit by an animal (Manly et al. 2002), which can then be plotted via geographic information systems (GIS) to provide a map of proportional probability of use. This map can then be used to draw ecological conclusions about a species, such as home range, distribution, or response to an environmental change.

The typical approach to RSFs is for the investigator to produce several potential models (sets of covariates) based on *a priori* knowledge of the species in question. Models are then evaluated against each other by means of an information theoretic approach (Burnham and Anderson 2002), by comparing values of Akaike's Information Criterion (AIC). Models are generally validated by testing their performance with other independent datasets, or by means of *k*-fold cross-validation (Boyce et al. 2002), which calculates a Spearman rank correlation coefficient (r_s) between *k* subsets of the data that were not used to generate the model, with higher values indicating a better model.

Resource selection functions have been applied in studies of many species, including birds (pileated woodpeckers – *Dryocopus pileatus*; Lemaître and Villard 2005), bears (grizzly bears – *Ursus arctos*; Nielsen et al. 2002), cervids (moose – *Alces alces*; van Beest et al. 2010) and bovids (bison – *Bison bison*; Fortin et al. 2009) among others. Multiple-species RSFs are also used to predict biodiversity at a site (Nielsen et al. 2003) or to model predator-prey interactions (Hebblewhite et al. 2005). Over the course of the last decade, the importance of the inclusion of multiple spatial scales of analysis in RSF-related research has become increasingly evident.

1.2 Spatial scale in ecological studies

The importance of incorporating scalar processes in the investigation of ecological phenomena has become evident over the past several decades, with Levin (1992) going so far as to suggest that scale is “the fundamental conceptual problem in ecology, if not in all of science.” Although some authors recognized problems relating to scale as far back as the turn of the 20th century (Johnstone 1908), the term *spatial scale* did not appear in the literature until the early 1970s (Marten 1972, Wiens 1973), and the growth of papers in *Ecology* and *Ecological Monographs* referencing more than one spatial or temporal scale grew exponentially in the 1980s, at a rate of 18.9% yr⁻¹ (Schneider 2001). The late 1980s and early 1990s saw many attempts to synthesize and solidify our knowledge of the role of scale in ecological processes (e.g., Wiens 1989; Kotliar & Wiens 1990; Levin 1992), and since the turn of the century there has been a great number of publications concerned with how to properly integrate our knowledge of spatial scaling in ecology to empirical studies (Boyce 2006, Meyer and Thuiller 2006, Mayor et al. 2009, Wheatley and Johnson 2009, DeCesare et al. 2012).

Scale is a difficult term to define, as its meaning has evolved over time and in actuality represents a suite of terms to describe the physical dimensions of an object in time or space (Hobbs 2003). Spatial scale in ecology is defined by two components, extent and grain. Extent is the size or length of an object in space or through time (Hobbs 2003) and in habitat selection studies it is examined by modifying the area deemed available to an individual or population. Grain is typically defined in one of two ways in the ecological literature: as the minimum mapping unit of landscape data (resolution or pixel size for raster data, Thompson & McGarigal 2002; Hobbs 2003); or as the size of a buffer area surrounding used and available telemetry

points (Anderson et al. 2005, Meyer and Thuiller 2006). Here, I use the latter definition of grain, while reserving the term “resolution” for the former. Scale may refer to either component.

Extent is typically defined by the framework established by Johnson (1980), who defined four hierarchical orders of selection made on increasingly smaller time frames ranging from the geographic range of the species to the selection of food items during foraging. Most RSF studies examine resource selection at either the 2nd or 3rd order, which define establishment of a home range and use within that home range, respectively. Each order in the hierarchy is linked to a different time scale in the life history of the species. First order selection (the geographic range of the species), is determined over the course of evolutionary and long-term climatic timescales, whereas fourth order selection is determined over minutes or seconds during feeding bouts.

Studies that explicitly incorporate spatial scale have shown that it is indeed important to examine. Animals have been shown to select resources at differing spatial scales (Kotliar and Wiens 1990, Schmidt 1993, Ward and Saltz 1994). Whittaker and Lindzey (2004) found that while resource selection at both the landscape-level (2nd order of selection) and fine-scale (diet-selection) level suggested competition between white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) over resources, differential selection at the home-range level suggested that the two species were establishing different home ranges and therefore not competing for resources. For herbivores, selection is often a trade-off between forage quality and abundance (Fryxell 1991, Van Der Wal et al. 2000, van Beest et al. 2010). At finer scales, herbivores tend to select for higher quality forage (Langvatn and Hanley 1993), however at broader scales forage abundance may be selected for (Månsson et al. 2007; van Beest et al. 2010).

Despite knowledge about the role of scale in our understanding of animal habitat use, most studies limit their focus to changes in extent, with grain being less frequently studied (but see review by Meyer and Thuiller 2006). In addition, habitat selection studies tend to focus on statistical hierarchies involved in scalar processes as opposed to examining underlying behavioural mechanisms relating to animal habitat use and movement.

1.3 Multi-grain resource selection functions

The scale at which an animal responds to its environment varies as a function of habitat type and behaviour; however, this is rarely incorporated into studies, even multi-scalar ones. Vigilance behaviour has been shown to vary by habitat type in mule deer (Altendorf et al. 2001) and red deer (*Cervus elaphus*, Jayakody et al. 2008)—suggesting a change in the size of the perceptual range of that individual. The perceptual range of an individual is defined as the distance from which an element on the landscape can be perceived or detected by an animal (Lima and Zollner 1996), defining the size of the sensory window to which animals may respond to objects on a landscape (Pe'er and Kramer-Schadt 2008). Spatial memory is likely to play a role in the relationship between scalar resource selection and habitat type. Animals navigate their environments via the formation of mental maps and the recognition of navigational beacons (Fagan et al. 2013). These cues are likely to be important at different scales across different habitats.

As such, we would expect different habitat types to be selected at different grains depending on the animal's perceptual range. Morris (1987) has suggested that individuals may be either coarse-grained (selection not proportional to availability) or fine-grained (selection proportional to availability) foragers (*sensu* MacArthur & Levins 1964) depending on the scale

examined; however, RSFs computed at multiple grains are typically focussed on integrating multiple selection orders (see review by Meyer and Thuiller 2006) or to account for potential location error in telemetry data (Rettie and McLoughlin 1999). Here, I introduce and evaluate the multi-grain RSF (MRSF), a process-based method to examine animal resource selection across multiple grains within selection orders to evaluate how an animal's perceptual range changes across habitat types.

1.4 Functional response

While resource selection functions allow us to test for habitat preference (Manly et al. 2002), relatively few studies of habitat selection factor in how the relative abundance of resources affects the strength of selection (see review by Godvik et al. 2009). The relative abundance of resources can have a significant effect on how they are selected by organisms. Differential selection based on resource availability is termed the functional response in habitat selection (Solomon 1949, Mysterud and Ims 1998). For example, if foraging sites are rarer in one region than in another, individuals may compensate by having a larger home range to include the same area of foraging sites, and given similar time budgets, would use these resources more relative to individuals with a greater proportion of foraging sites within their home range (Mysterud and Ims 1998).

A common method of quantifying functional response is by the use of selection ratios (Manly et al. 2002, Herfindal et al. 2009), which calculate a ratio of used points to available points for a resource type. By taking the log of this value an index is produced in which positive values indicate selection and negative values indicate avoidance. By calculating this ratio for

many individuals, the functional response can be quantified by plotting resource availability against the log of the selection ratio.

1.5 White-tailed deer

White-tailed deer are a semi-gregarious cervid with a wide-spread distribution, having populations ranging from central North America to northern South America (Hirth 1977). Like most social ungulates, white-tailed deer exhibit sexual segregation outside the autumn rutting season (Marchinton and Hirth 1984), with males tending to be solitary and females frequently accompanied by their young-of-year and often their female yearlings as well (Marchinton and Hirth 1984). In winter, deer often display yarding behaviour, associating with each other in close proximity.

Determining preferred white-tailed deer habitat is difficult, owing to the fact that deer are found in a great variety of habitat types and are adaptable to exploiting a large variety of food resources across the extent of their range, and are therefore considered to be habitat generalists (Harlow 1984, Marchinton and Hirth 1984). White-tailed deer food preference is affected by many factors, including population density, climate and plant availability (Harlow 1984). At northern latitudes, white-tailed deer often exhibit short-distance seasonal migration from a summer to a winter range (Nelson 1998). This migration has typically been explained by nutritive and thermal requirements due to snow cover (Severinghaus and Cheatum 1956), however an anti-predator function to migration and yarding behaviour has also been proposed (Messier and Barrette 1985, Nelson and Mech 1991).

Hirth (1977) has suggested that habitat selection by deer is predicated on trade-offs between forage access and availability and predator avoidance. The theory posits that solitary

deer or those in small groups face reduced risk of predation in woodland environments but in doing so forego more valuable forage in open environments. This advantage due to crypsis would be lessened with larger groups, while the benefits of foraging on open habitats would be increased due to group vigilance, e.g., with more individuals watching for predators, each individual can be less vigilant and spend more time feeding (Childress and Lung 2003, Lung and Childress 2007), which has been shown to increase intake rate (Fortin et al. 2004). In addition, risk of predation for each individual is lessened due to prey dilution (if the group is attacked successfully by a predator, the probability of a certain individual being preyed upon is reduced as group size increases — lowering the perceived risk for each individual; Clutton-Brock et al. 1982).

Cervids are often considered to be a nuisance species to agriculture, resulting in crop damage on agricultural fields (Brook 2009, Sorensen et al. 2014), with the threat of disease transmission from free-ranging individuals to domestic herds being an ever-present concern (VerCauteren et al. 2010).

1.6 Research goals and hypotheses

My goals for this M. Sc. project were to examine resource selection patterns of white-tailed deer in and around Riding Mountain National Park, Manitoba, Canada, across multiple spatial scales and seasons. Due to collar failure during the progression of the study, the number of individuals examined varied as a function of season. This thesis is presented in a manuscript style. In Chapter 2, I examine how changing grain size for each covariate affects resource selection patterns across two extents (landscape level and within-home-range) and seasons (summer and winter) to produce multi-grain resource selection functions. The goal of my third

chapter was to examine how grain size affects detection of functional responses in habitat selection. An overall summary and conclusion is presented in Chapter 4.

My thesis takes an information-theoretic approach to data analysis. The analysis of complex ecological data with multiple causal factors is often unsuited to classical hypothesis testing with a null hypothesis, as is model selection techniques using AIC and information theory (Burnham and Anderson 2002, Elliott and Brook 2007). As such, I take the approach of multiple working hypotheses suggested by Chamberlin (1890). I produced multiple competing models (e.g., hypotheses on animal habitat selection), and use information theory informed by the multiple working hypotheses concept to generate and evaluate white-tailed deer resource selection.

I hypothesized that if an individual's perceptual range varied by habitat type, then model parameters would be both grain- and habitat-dependent. As such, I predicted that selection for covariates would change as grain of analysis changed, and that each resource would be selected or avoided (or neither) at different grains, and consequently that MRSFs would be more predictive than single-grain models. I also predicted that selection would differ across the two extents (2nd and 3rd order) analyzed and that the landscape-level models would be more predictive at larger grains than the within-home-range models. For my functional response analyses I predicted that functional responses would be dependent on grain size and that at the largest grains functional responses would weaken as grain size increases to the point where used and available points become more similar.

Chapter 2: Process-focussed, multi-grain resource selection functions

2.1 Abstract

Like most aspects of ecology, the process of habitat or resource selection scales in space and time. However, scaling questions have generally focused on extent including size of study area and home ranges that dictate availability of resources; grain of analysis (size of resource units used) is generally restricted to questions of methodology as opposed to functional ecology. Most often, grain is adopted as a point, unit, or patch that is common in size to all habitat resources used and available; however, in the process of habitat selection, it is feasible that individuals may opt to select for different resources at different grains. For example, animals may use units of vegetation association at a finer grain when feeding or resting compared to when moving through habitat. Here I introduce and evaluate the ‘multi-grain resource selection function’, or MRSF. I generated MRSFs for a case study of GPS-collared white-tailed deer (*Odocoileus virginianus*; $n = 14$) at Riding Mountain National Park, Manitoba, Canada. I created models across two seasons and extents and varied the radius around used and available points within which resource types were measured, and compared models to evaluate the relative importance of resource variables at different grains. I hypothesized that resource selection would change with grain, and that RSFs computed using multiple grains would be more predictive than models computed using a single grain as they better incorporate the space of influence on decision making in different habitat areas. I found that models of animals using grains of different sizes for different resource types

were characterized by comparatively lower AIC and better cross-validation scores. I conclude that scaling grain can and should be considered in models of resource selection, and that animals make decisions on resource selection at multiple grains. The MRSF, like analyses incorporating individual effects, density dependence, and functional responses, brings us closer to incorporating process into the study of resource and habitat selection.

2.2 Introduction

The concept of scale is central to the study of how animals interact with their environment (Wiens 1989, Levin 1992, Wheatley and Johnson 2009). Scale of analysis has been shown to affect resource selection patterns (Boyce et al. 2003, Anderson et al. 2005, Meyer and Thuiller 2006, Ciarniello et al. 2007, Leblond et al. 2011), interspecific competition (Whittaker and Lindzey 2004), and detection of sexual segregation (Bowyer et al. 1996). Life history traits may be scale-sensitive (Bowyer and Kie 2006) and decisions on where to establish a home range may be different from decisions relating to the use of that home range (Apps et al. 2001, Johnson et al. 2001).

Spatial scale is defined by two components: extent and grain (Hobbs 2003). In the study of habitat selection, extent is studied by modifying the area deemed available to organisms and is typically defined by the framework established by Johnson (1980), who identified four hierarchical orders of selection made on increasingly shorter time scales ranging from the geographic range of the species to the selection of food items during foraging. Most models of habitat selection are conducted at either the 2nd or 3rd order, which define establishment of a home range and use of resources within that home range, respectively. Grain is defined as the minimum mapping unit of landscape data (resolution or pixel size for raster data, Thompson and

McGarigal 2002, Hobbs 2003), or sometimes as the size of an area surrounding points of observation within which ecological data are considered (Anderson et al. 2005, Meyer and Thuiller 2006).

Considerations of spatial scale are intimately linked to temporal scale, with decisions made at longer temporal scales being linked to larger spatial scales (Holling 1992). Wiens (1989) defined a domain of habitat selection as a range of scales over which ecological patterns are similar, and Thompson & McGarigal (2002) proposed that habitat can be viewed as a spectrum which shifts in response to changing scale. It should, therefore, be possible to identify thresholds in selection domains by examining a continuum of spatial scales, with those thresholds representing scales where the relative abilities of different factors to limit fitness become reversed (Rettie and Messier 2000). Changing extents modifies what resources are deemed available to individuals, whereas changing grain size modifies how a selected (or available) resource is defined and subsequently perceived by an animal (e.g., “landscape context variables” *sensu* Leblond et al. 2011).

Despite acknowledging the importance of scale on the process of habitat selection, most researchers on the subject typically approach the study of scale from the perspective of examining statistical hierarchies as opposed to examining underlying mechanisms behind patterns. It is not unreasonable to expect the scale at which an animal responds to its environment to vary as a function of habitat type and behaviour. For prey animals, for example, vigilance behaviour has been shown to vary by habitat type (e.g., mule deer [*Odocoileus hemionus*], Altendorf et al. 2001; red deer [*Cervus elaphus*], Jayakody et al. 2008)—suggesting that a change in the size of the perceptual range of an individual across habitats should affect behaviour. An animal travelling through or feeding in an enclosed habitat such as forest will be

selecting habitat on a smaller scale than an individual travelling or foraging in open habitats, where vigilance and consideration of cover become increasingly important at larger spatial scales. As such, different habitat types should be selected at different grains depending on the animal's perceptual range. This idea is not new. Indeed, Morris (1987) argued that individuals may be either coarse-grained or fine-grained foragers (*sensu* MacArthur and Levins 1964) depending on the scale examined. However, incorporating this insight into contemporary models of habitat selection is lacking.

Today the most common method of studying animal resource selection is by means of the resource selection function, or RSF (Manly et al. 2002). RSFs compute a relative probability of habitat use by regressing a set of used and available (or unused) resources against a set of explanatory variables. Where RSFs have been computed at multiple grains for a given extent, the modelling has typically focussed on integrating multiple selection orders (see review by Meyer and Thuiller 2006) or to account for potential location error in telemetry data (Rettie and McLoughlin 1999). As such, these studies fail to account for how context-dependent isotropic perceptual range (*sensu* Olden et al. 2004) might affect resource selection patterns. Here I introduce and evaluate what I term the multi-grain RSF (or, MRSF) as a process-based method to examine animal resource selection across multiple grains within selection orders to evaluate how an animal's perceptual range changes across habitat types.

Consideration of the context of a resource unit can have a profound effect on resource selection. For example, the white-tailed deer (*Odocoileus virginianus*) is a large herbivore known to select for edge habitat (Williamson and Hirth 1985). By modelling resource selection at only the smallest grain (e.g., at a single point in space), researchers risk generalizing potentially distinct resource types that may vary in quality for an animal based on their ecological context

(e.g., surrounding vegetation associations). This relationship can be expected to vary temporally as well, as different seasons are likely to generate different scalar relationships as resource availability changes (Pearson et al. 1995). The challenge facing ecologists is to determine what factors are important at what scales and to properly integrate knowledge across multiple scales (Turner et al. 1989), examining both grain and extent to obtain accurate information on animal space-use patterns.

I generated and evaluated MRSFs for a sample of white-tailed deer in Manitoba, Canada. Deer were located at the interface of a forested wildlife preserve (Riding Mountain National Park) and a surrounding agricultural matrix. Deer were tracked by Global Positioning System (GPS) collars for one year in both winter and summer and at two different extents: within-home-range (3rd order *sensu* Johnson 1980) and at the landscape level (2nd order *sensu* Johnson 1980). White-tailed deer are found through large parts of eastern North America, and inhabit a range of habitats and exhibit short-distance seasonal migrations in northern latitudes (Nelson 1998, Van Deelen et al. 1998). For each RSF model, I quantified resource selection at multiple grain sizes by using buffers of increasing radius around telemetry and random locations. My goal was to examine how resource selection for individual covariates changed with changing grain size and develop a model for each season/scale that would incorporate multiple grains to detect thresholds in habitat selection domains. I hypothesized that due to changing spheres of perception across habitat types, resource selection model parameters would vary with habitat type and grain size. I predicted that selection for covariates would change as grain of analysis changed (P_1), and that each resource would be selected or avoided (or neither) at different grains (P_2). As a result, I predicted that MRSFs would be more predictive than single-grain models (P_3). I also predicted that, as in other studies (Anderson et al. 2005) selection would differ across the two extents (2nd

and 3rd order) analyzed (P₄) and that the landscape-level models would be more accurate at larger grains than the within-home-range models (P₅), reflecting decisions made at larger spatial scales (grains) at the landscape-level.

2.3 Methods

2.3.1 STUDY AREA

My study area was located in southwest Manitoba, Canada, and contained two distinct habitats: the forest-dominated area within Riding Mountain National Park (RMNP) and the surrounding agriculture-dominated matrix. RMNP (2,974 km²) is a protected area that consists of eastern deciduous forest, northern boreal forest, and rough fescue grasslands with sporadic wetlands (Rowe 1972, Caners and Kenkel 2003). Higher elevations in the park are dominated by spruce (*Picea* spp.) and pine (*Pinus banksiana*), while aspen (*Populus tremuloides*) is common throughout the park. The area surrounding the park is intensively managed for the production of annual cereal and oilseed crops, perennial forage crops and beef cattle (Brook 2010), and is interspersed with small fragmented patches of native deciduous forest, wetland and grassland (Fig. A1).

The area is populated by a diversity of wildlife species, including elk (*Cervus canadensis*), moose (*Alces alces*), and a panmictic population of white-tailed deer (Brook and McLachlan 2006, Vander Wal et al. 2013). Predators in the area include wolves (*Canis lupus*), black bears (*Ursus americanus*), lynx (*Lynx canadensis*) and coyotes (*Canis latrans*).

2.3.2 DATA COLLECTION AND HABITAT VARIABLES

Adult white-tailed deer ($n = 12$ female and 2 male in spring, 7 female in winter) were captured via a net gun fired from a helicopter (Cattet et al. 2004, Brook et al. 2013) in February 2006 and fitted with GPS-tracking collars. Collars were active for one year. Individuals were captured in the northern part of RMNP and the agricultural area just outside of the northern boundary of RMNP but were free to enter or exit the park along the entire park boundary. A total of 12,573 locations (3287 in RMNP and 9286 in the surrounding agriculture) were collected across the two seasons, with a mean of 599 (SE = 87.7) locations per animal per season. Animal capture and handling was conducted in accordance with the guidelines of the Canadian Council on Animal Care, University of Alberta protocol ID# 472702.

My goal was to construct and evaluate MRSFs at two extents (landscape-level and within-home-range) to determine how habitat selection varied as grain size changed. For the within-home-range analyses, I created seasonal (summer and winter) 95% minimum convex polygon (MCP) home ranges (Osco et al. 2004, van Beest et al. 2010) for each deer ($n = 21$ animal seasons). I delineated seasons based on movement rates as defined by van Beest et al. (2013), who used periods of increased movement of individuals to determine seasonal transition dates. I buffered home ranges by 327 m (the mean distance travelled between successive GPS fixes) to better reflect the area available to individuals. Within each individual's buffered home range I generated random points equal to the number of GPS fixes. At the landscape level, I generated a 100% MCP surrounding all telemetry points of the study animals and buffered it by 327 m. MCPs are frequently used in RSF analyses as a simple and objective method to delineate all areas used and available to individuals (Godvik et al. 2009, Herfindal et al. 2009). I generated random points to match each individual within this polygon. Telemetry points located in lakes

were removed ($n = 12$) as unlikely deer habitat and lakes were excluded when generating random points. Lakes were, however, included as a covariate in the analysis to evaluate use of lake edges (e.g., points excluded lakes, but buffers surrounding points could encompass lake habitat).

To determine which grains best predicted white-tailed deer use, I quantified several environmental covariates in concentric buffers around used and available points at radii of 75, 150, 327, 500, 750 and 1000 m using ArcMap (ArcGIS 10.1, ESRI Redlands, California, USA) and Geospatial Modelling Environment (Beyer 2012). Land cover was assessed using 30 m resolution Landsat 5 satellite imagery (Geobase: <http://www.geobase.ca>). Field validation performed in 2011 showed that 84% of validated points were accurate, with most misclassified points being due to changes in agricultural cropland (Dugal 2012). Within each buffer I calculated the proportion of forest, perennial cropland, grassland, wetland and water as well as density of streams and unpaved roads ($\text{m} \times \text{ha}^{-1}$). I evaluated several methods of quantifying habitat heterogeneity. I calculated total edge density, Shannon's Diversity Index, Simpson's Diversity Index and contagion within my buffers. Diversity indices were based on the diversity and abundance of habitat types within the buffers. Due to correlation between these metrics, I could only use one in my analyses; I chose to use Simpson's Diversity Index because it was most descriptive of white-tailed deer presence in the majority (~95%) of my preliminary analyses. All variables were centred by dividing each observation by the mean value of the variable.

2.3.3 STATISTICAL ANALYSES

I used resource selection functions (Manly et al. 2002) using a used/available design. My landscape-level analyses corresponded to a type II design, where individuals are identified but availability is defined at the population level, whereas my within-home-range analyses

corresponded to a type III design, since availability was also defined for each individual (Thomas and Taylor 2006). I screened my explanatory variables at each buffer size, and ensured that none of the variables selected for analysis were highly correlated ($r > |0.7|$) or had a variance inflation factor greater than five. RSFs calculate a relative probability of use for each resource (pixel) as:

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 \dots \beta_n x_n) \quad (2.1)$$

where β_n is the coefficient of variable x from the regression model and x_n is the value of variable x for that pixel. I used generalized linear mixed-effects modelling implemented in R (R Development Core Team 2012) with package lme4 (Bates et al. 2012) using individual white-tailed deer as a random effect in my RSF models to account for variation between individual white-tailed deer, number of locations for each deer, as well as for different habitat availability for different individuals (Gillies et al. 2006). Due to complications with lack of convergence and to ensure that models were simple enough to successfully run across all grain sizes, I decided to not examine interactions.

I performed three analyses on each of my four (two selection orders \times two seasons) global models across a total of six grain sizes. These data were used both to analyze the effect of changing grain on resource selection as well as to inform decision-making for construction of MRSFs. In the first analysis I quantified the importance of the variable to the overall global model at each grain by calculating the effect on Akaike's Information Criterion (AIC) of removing the variable from the global model:

$$\Delta AIC_{\text{variable}}(x) = AIC_{\text{global model} - \text{variable}(x)} - AIC_{\text{global model}} \quad (2.2)$$

Negative values indicated that inclusion of the variable improved the model, and positive values suggested that inclusion of the variable weakened the model. Second, I used R package MuMIn

(Bartoń 2013) to calculate model-averaged β -coefficients and standard errors across all possible models. Thirdly, I used the MuMIn package (Bartoń 2013) to determine variable importance, defined as the sum of the AIC weights ($AICw_i$) of all models in which the variable in question appears, providing a value between 0 (values approaching 0 have very low importance) to 1 (values approaching 1 have very high importance, Burnham and Anderson 2002).

To construct my final RSF models, I assessed evidence from all three analyses to determine which grain size was most explanatory and subsequently which grain size to use as covariates in my final model. When evidence as to which grain size was most important to the model varied among analyses or was very close, I compared models using each and chose the grain size that resulted in the lowest AIC in the final model. When a variable had a different sign at different grains of analysis, I included both terms in my models, provided the two were not excessively ($> |0.7|$) correlated. I dropped variables that resulted in a decrease in AIC, dropping variables that resulted in the greatest drop in AIC first. The resulting models were mapped using ArcMap. RSF maps were scaled to between 0 and 1 by dividing the RSF value by 1 plus the RSF value. I compared my MRSFs to my best (lowest AIC) single-grain models at each season/extent by comparing AIC values (across scales) and plotting a Δ RSF value map in ArcMap, subtracting RSF values of my best single-grain model from my multi-grain model to quantify how resource selection patterns changed when multiple grain sizes were considered. I used the k -fold cross-validation method proposed by Boyce et al. (2002) to evaluate the predictive success of my models (validation was performed within-individual [Boyce et al. 2002], but see [Koper and Manseau 2009]). This method calculates a Spearman rank correlation coefficient (r_s), with higher values indicating a better model.

2.4 Results

My results show that white-tailed deer selected different resources at different grains. For most of the covariates analyzed, the grain size at which the greatest drop in AIC was observed when adding the focal variable to a quasi-global model was the best grain size to use in the final model. Lowest AIC values corresponded with large (positive or negative) β -coefficients with small confidence intervals (Fig. 2.1). Low AIC values were associated with high variable importance as determined by the sum of Akaike weights of all models including the variable. However, the latter analysis proved to be less important in model construction as in many cases the value would be ≈ 1 across all grain sizes (e.g., wetland in winter at 2nd order extent [Fig. 2.1]).

The grain that best explained white-tailed deer use or avoidance varied among different covariates. White-tailed deer selected for forest habitats and grassland habitats, the former at small grain sizes (75 or 150 m), the latter at large grain sizes (1000 m) in the winter and small grains in the summer (Tables 2.2 and 2.3). White-tailed deer selected for areas with high values of Simpson's Diversity Index at intermediate (150 and 327 m) grains. Lake edges were avoided, with large grain sizes being most predictive. Selection of roads, streams and wetlands was grain-dependent and varied across seasons/extents analyzed (Figs 2.2 and 2.3).

I found grain to significantly affect resource selection, supporting P_1 . Across 32 covariates analyzed (8 covariates \times 2 seasons \times 2 selection orders), all had confidence interval (CI) estimates at one grain size that did not significantly overlap the CI at at least one other scale at the $\alpha = 0.05$ level (had non-overlapping 84% CIs; Julious 2004; Figs 2.2 and 2.3). Variable importance and ΔAIC values also varied with changing grain size. In 7 covariates (19.4%), animals either significantly selected or avoided the resource depending on grain analyzed (had at least one positive and one negative β -coefficient where the 95% CI did not overlap zero).

The most accurate grain varied across covariates, supporting P_2 and suggesting that white-tailed deer make space-use decisions at different scales for different resources. Across both seasons/extents analyzed the MRSF had a lower AIC score than any single-grain model. In three of the four seasons/extents analyzed, the cross-validation score was higher than any of the models computed using only a single grain of analysis (Table 2.3). Δ RSF scores between the best single-grain model and my multi-grain models (Fig. 2.4, c + d) suggested that using a multi-grained approach to resource selection functions results in significant differences in resource selection patterns.

The magnitude of resource selection varied with changing extent, providing moderate support for P_3 . Of 96 data points analysed (6 grains \times 2 seasons \times 8 covariates), 67 (69.8%) had 84% confidence intervals at the two extents that did not overlap (Figs 2.2 and 2.3), providing some support for P_3 . However, the best grain for each covariate generally remained the same across seasons and extents, rejecting P_4 that larger grains would be more important at the 2nd order of selection.

2.5 Discussion

A central focus of ecological studies is the question of how spatial scale informs patterns of habitat selection (Senft et al. 1987, Levin 1992). The distinction between fine-grained (use proportional to availability) and coarse-grained (selection disproportional to availability) foraging strategies *sensu* MacArthur & Levins (1964) is known to be scale-dependent (Morris 1987). I hypothesized that by examining multiple grains it would be possible to distinguish thresholds in which individuals transition from being coarse-grained foragers (e.g., selectors) at one spatial scale to fine-grained foragers at another, and that individuals could be found to be

simultaneously fine-grained foragers for one resource and coarse-grained foragers for another resource at the same spatial scale (grain).

I found that selection of resources changed with grain and that optimal grain size for predicting white-tailed deer presence differed depending on the resource, suggesting they made decisions at different spatial scales for each resource, supporting P_1 and P_2 . Forests were selected at smaller grains compared to agricultural habitats or grassland habitats (in the summer), suggesting a change in the animal's perceptual range in different habitats and across seasons, relating to both activity type (foraging versus bedding) and habitat type (e.g., individuals can see farther in open habitats). Equally important is an individual's spatial memory of its environment. To navigate successfully across a landscape, individual animals form a mental map of their surroundings, using cues to navigate (Fagan et al. 2013). I found that the best grain to model resource selection was habitat-dependent, suggesting that each habitat type informs animal movements at different scales and that cues informing an animal's cognitive map change scale in different habitats. The importance of cognitive spatial memory on our interpretation of scalar processes in animal resource selection remains underappreciated. Grain-dependent resource selection may also reflect variability in how resources are selected temporally. Johnson's (1980) hierarchy of scales posits that decisions made by animals at larger spatial scales will be made over longer time frames. Cover habitat, which was selected for at smaller grains, is likely important over very short timeframes when an animal feels threatened, whereas forage resources are important over much longer timeframes and subsequently selected at larger grains.

In some cases, selection changed sign as grain increased (e.g., stream density). This likely reflected a trade-off in the optimal distance to or density of a resource. Scales where selection changes sign may represent threshold scales at the border of domains of animal behaviour

(Wiens 1989); these scales should reflect points on a continuum of scales where the influence of the resource on individual fitness become reversed (Rettie and Messier 2000). White-tailed deer may have avoided streams on small scales due to factors such as predation pressure that may be associated with open areas surrounding streams but selected them at larger scales as a potential water resource. In this instance, white-tailed deer were acting as coarse-grained foragers at intermediate scales and as fine-grained foragers at both small and large scales, supporting Morris' (1987) assertion of foraging activity being scale-dependent. By including two covariates for a single resource computed at different grain sizes, I successfully incorporated attributes of two distinct fine-grained foraging behaviours in my models.

My study found important differences in resource selection across grain sizes and found that multi-grain models were more predictive than models built using only a single grain of analysis, supporting P₃. Anderson et al. (2005) failed to detect influences of grain size on resource selection in elk, and attribute the lack of grain dependence in resource selection in their study to a narrow environmental gradient length. This could have played a more important role in my study, which was conducted at the interface of managed parkland and a highly fragmented agricultural landscape.

While extent has been shown to be very important in affecting resource selection patterns (Anderson et al. 2005), my results suggest that extent was less important than grain size in informing resource selection patterns of white-tailed deer. In many cases (Simpson's Diversity in both seasons, grassland in winter; see Figs 2.2 and 2.3), selection remained nearly constant across the two extents analyzed; however, large variations were evident as grain size was altered. I hypothesized, as other studies have (DeCesare et al. 2012), that larger grain sizes would be more explanatory at larger extents. My results indicate that this was not the case for this

population; the best grain tended to remain the same across extents (the exception being water and wetland in summer; see Table 2.1), providing only marginal support for P_4 and rejecting P_5 . This suggests that for this population, and potentially many others, the grain component of scale may be more important to study than the extent component.

The three analyses I used to determine variable importance across grain sizes proved useful in developing my final models. The sum of cumulative $AICw_i$ for all models proved to be predictive of what grain size to use in construction of my final models, however in many cases $AICw_i \approx 1$ across many, if not all, grain sizes. Secondly, I used a novel technique which evaluated the relative difference in AIC between a global model and a quasi-global model excluding the variable in question. This analysis performed well; the grain size that had the greatest drop in AIC with the addition of the variable in question generally ended up being the best grain size to use in my final model and was more sensitive than using $AICw_i$. This metric usually coincided with the largest β coefficients; however, in some cases smaller β coefficients were more predictive depending on standard errors. These three analyses were instrumental in generating my final, multi-grain models.

Biologically relevant habitat heterogeneity is an important factor in determining how scale relates to animal resource selection (Boyce et al. 2003). Without heterogeneity in landscapes, scaling in ecology would be a trivial matter, and it does appear that more homogeneous landscapes may result in less detection of scalar processes in resource selection (Schaefer and Messier 1995). Consequently, the scale at which animals make habitat selection decisions is intimately linked to the level of fragmentation of a landscape. White-tailed deer are known to be dietary and habitat generalists and to select for edge habitat (Williamson and Hirth 1985), a conclusion supported by the fact that deer selected for areas with a high Simpson's Diversity

Index. Landscape heterogeneity has been shown to influence home range size in both mule (Kie et al. 2002) and white-tailed deer (Dechen Quinn et al. 2012). Across all analyses, diversity was most explanatory at intermediate grains (150 and 327 m). This could be due to the fact that diversity had the highest variance (s^2) at these grain sizes (Fig. A2), where grain size was large enough to detect heterogeneities in the landscape but not so large that this variability was lost. As such, the most descriptive grain in illustrating animal habitat selection is linked to the level of fragmentation and heterogeneity of that habitat.

Despite the fact that the importance of scalar processes on animal resource selection is well known, the incorporation of grain size into models of animal space use remains underappreciated, especially in the context of process-based, behaviourally-focussed resource selection across habitat types due to changing spheres of animal perception. There have been many advances in our understanding of how animal resource selection should be modeled. These advances include revelation of functional responses in animal habitat selection (Mysterud and Ims 1998), the inclusion of random effects to account for individual variation (Gillies et al. 2006) and the consideration of important population dynamics such as population density (McLoughlin et al. 2010, van Beest et al. 2014). The process-focussed, multi-grain resource selection function introduced here represents a key step forward in our ability to incorporate behavioural processes into the study of animal distributions.

Tables and figures

Table 2.1. Top five multiple-grain models for each season/scale for white-tailed deer in the RMNP region, 2006–2007. Model construction was performed using evidence from single-grain analyses. Numbers represent the grain (m) used to construct the model.

Model	Rank	Forest	Grass-		Roads	Diversity	Streams	Water	Wetland	d.f.	Log L	Δ AIC
			land	Perennial cropland								
Winter,	A	75	1000	75, 500	–	150	150	1000	–	9	–4277.7	0.0
2 nd order	B	75	1000	75, 500	–	150	150	1000	500	10	–4277.1	0.8
	C	75	1000	75, 500	–	150	150	1000	327	10	–4277.1	0.8
	D	75	1000	75, 500	750	150	150	1000	500	11	–4276.5	1.6
	E	75	1000	75, 500	750	150	150	1000	327	11	–4276.6	1.7
	N	–	–	–	–	–	–	–	–	2	–6752.6	4936
Winter,	A	75	1000	500	750	150	327	1000	1000	10	–5768.8	0.0
3 rd order	B	75	1000	500	500	150	327	1000	1000	10	–5768.9	0.2
	C	75	1000	750	500	150	327	1000	1000	10	–5769.5	1.4
	D	75	1000	500	750	150	327	1000	327, 1000	11	–5768.8	2.0
	E	75	1000	500	500	150	327	1000	327, 1000	11	–5768.9	2.2

	N	–	–	–	–	–	–	–	–	2	–6752.6	1950
Summer,	A	150	75	500	–	327	75, 750	1000	1000	10	–9021.4	0.0
2 nd order	B	75	75	500	–	327	75, 750	1000	1000	10	–9021.7	0.7
	C	75	75	500	1000	327	75, 750	1000	1000	11	–9021.2	1.6
	D	150	75	500	1000	327	75, 750	1000	1000	11	–9021.3	1.8
	E	75	75	500	150, 1000	327	75, 750	1000	1000	12	–9021.1	3.4
	N	–	–	–	–	–	–	–	–	2	–10677.2	3296
Summer,	A	75	75	500	75, 1000	327	75	327	327	11	–9686.7	0.0
3 rd order	B	75	75	500	150, 1000	327	75	327	327	11	–9686.9	0.5
	C	75	75	500	1000	327	75	327	327	10	–9688.4	1.4
	D	75	75	500	1000	327	75	–	327	9	–9696.3	15.2
	E	75	75	500	–	327	75	–	327	8	–9707.8	36.3
	N	–	–	–	–	–	–	–	–	2	–10677.2	1963

* Dashes indicate variables that were not present in the model. N= Null model.

Table 2.2. Resource selection function models for white-tailed deer in the Riding Mountain National Park region, 2006–2007.

Model	→	Winter 2nd			Winter 3rd			Summer 2nd			Summer 3rd		
Variable	Grain	β	SE	Grain	β	SE	Grain	β	SE	Grain	β	SE	
(Intercept)	NA	−3.309	0.148	NA	−2.516	0.206	NA	−1.263	0.076	NA	−1.235	0.128	
Forest	75	0.509	0.026	75	0.339	0.019	150	0.436	0.020	75	0.236	0.030	
Grassland	1000	2.486	0.058	1000	1.680	0.071	75	0.395	0.016	75	0.269	0.015	
Per. crop	75	0.024	0.007	500	−0.195	0.015	500	−0.127	0.008	500	−0.089	0.007	
28 Roads	500	−0.152	0.016	—	—	—	—	—	—	—	—	—	
	—	—	—	750	−0.095	0.036	—	—	—	75	−0.010	0.005	
	—	—	—	—	—	—	—	—	—	1000	0.226	0.043	
Diversity	150	0.692	0.042	150	0.816	0.039	327	0.835	0.037	327	0.850	0.041	
Streams	150	0.045	0.012	327	−0.093	0.015	75	0.054	0.008	75	0.052	0.008	
Water	—	—	—	—	—	—	750	−0.168	0.024	—	—	—	
	1000	−0.278	0.029	1000	−0.090	0.009	1000	−0.235	0.013	327	−0.012	0.003	
Wetland	—	—	—	1000	0.189	0.024	1000	0.116	0.015	327	−0.113	0.013	
r _s	0.990			0.969			0.986			0.902			

* Dashes indicate variables that were not present in the model.

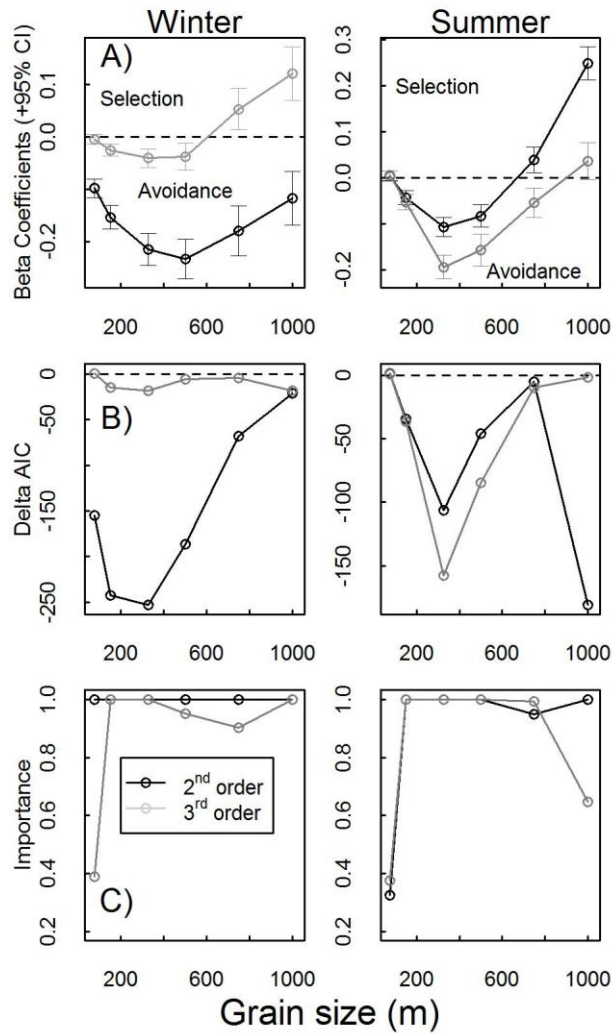
Table 2.3. Degrees of freedom, ΔAIC and k -fold cross-validation scores for models computed at six single grain sizes and one computed using multiple grains for white-tailed deer in the RMNP region, 2006–2007. Single-grain models represent the best model for each grain size, based on analysis of all possible models. Multiple-grain models were constructed using evidence from multi-model inference techniques on single-grain models.

Model	Grain (m)	d.f.	ΔAIC	r_s^*
Winter, 2 nd order	Multiple	9	0.00	0.990
	1000	9	489.13	0.969
	750	10	840.02	0.984
	500	9	1398.81	0.977
	327	10	1731.07	0.945
	150	10	2127.67	0.850
	75	10	2917.84	0.821
Winter, 3 rd order	Multiple	10	0.00	0.976
	150	10	694.85	0.965
	327	10	744.77	0.934
	1000	8	823.46	0.904
	75	9	915.38	0.966
	500	10	939.13	0.937
	750	10	993.83	0.969
Summer, 2 nd order	Multiple	10	0.00	0.986
	150	10	827.91	0.975
	75	9	833.33	0.953

	327	9	1056.54	0.976
	500	10	1708.26	0.948
	1000	9	1997.31	0.922
	750	9	2039.77	0.928
Summer,	Multiple	11	0.00	0.902
3 rd order	75	8	66.33	0.960
	150	10	198.33	0.984
	327	9	579.10	0.727
	500	8	1210.81	0.625
	750	9	1625.51	0.748
	1000	10	1670.09	0.608

* k -fold cross-validation score using 5 testing / training sets and 10 bins.

Fig. 2.1. Three analyses of wetland resource selection across multiple grain sizes by white-tailed



deer ($n = 14$ in summer, 7 in winter) in the Riding Mountain National Park area in 2006–2007 across two seasons and spatial extents. Left panels are winter selection and right panels are summer selection. Black symbols represent 2nd order selection and grey symbols represent 3rd order selection. A) Model-averaged covariate values with 95% confidence intervals. Dashed line represents the intercept (no selection or avoidance). B) The effect on AIC score of adding wetland to a quasi-global model (see Methods for details of computation). Values beneath the dashed line indicate that adding the variable to the model improves the

model (lowers the AIC); values above the dashed line indicate that adding the variable to the model results in a weaker model. C) Variable importance, defined as the sum of cumulative $AICw_i$ for all models containing the variable. A value of 1 indicates the variable is important in all top models.

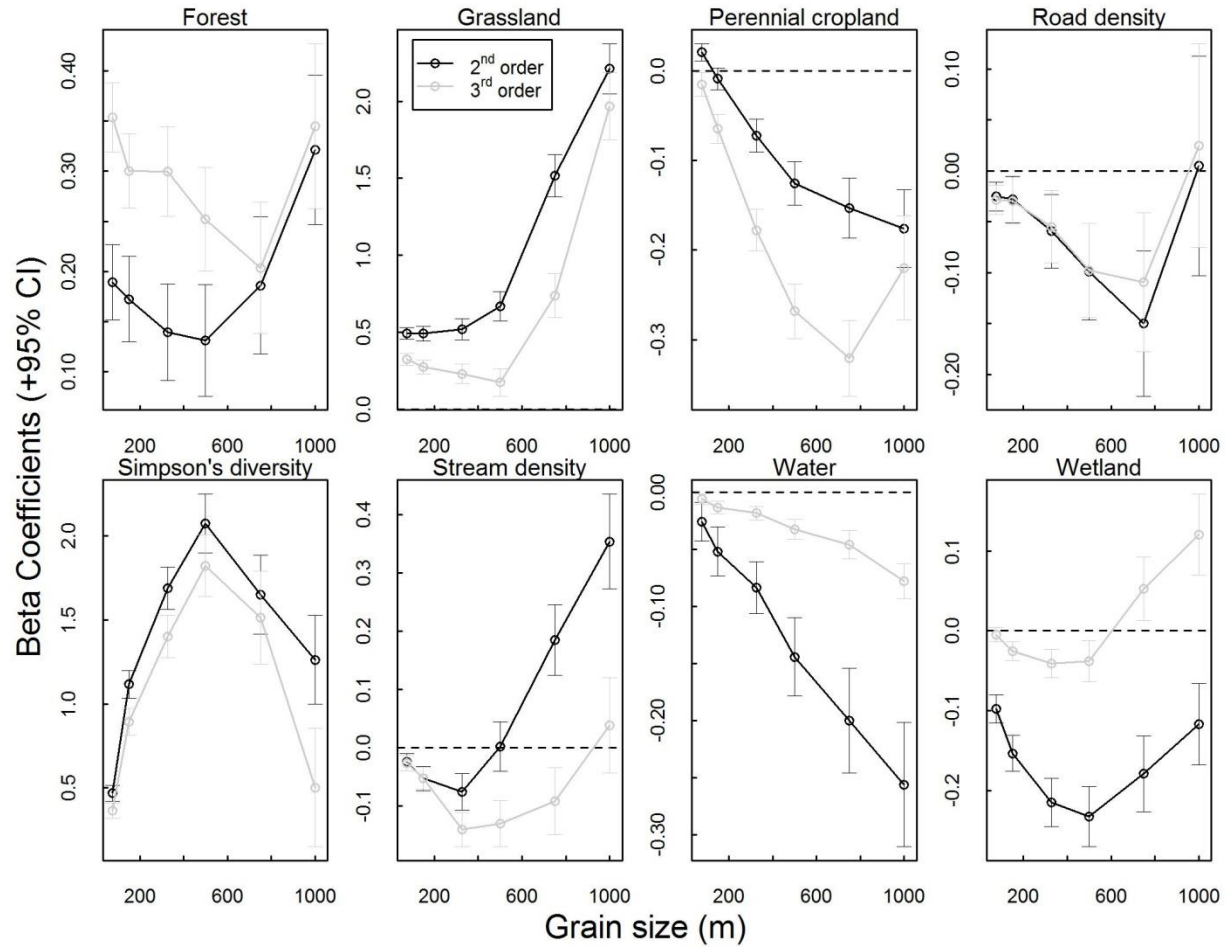


Fig. 2.2. Winter model averaged resource selection values and 95% confidence intervals across multiple grain sizes for white-tailed deer ($n = 7$) in the Riding Mountain National Park region, 2006–2007. Black symbols represent 2nd order selection and grey symbols represent 3rd order selection. Values are model averaged values based on all possible models run using multi-model inference (see Methods for details). Dashed line represents the intercept (no selection or avoidance).

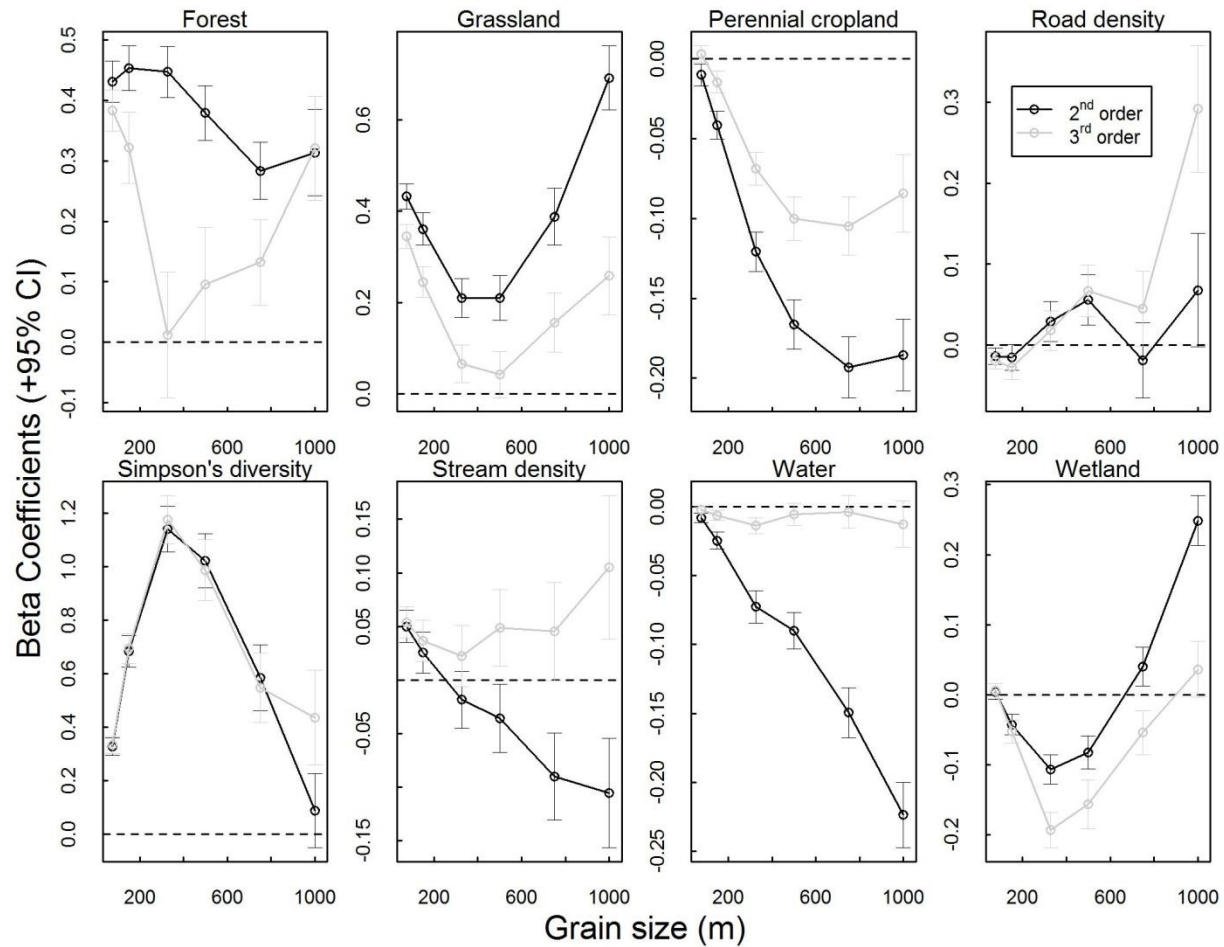


Fig. 2.3. Summer model averaged resource selection values and 95% confidence intervals across multiple grain sizes for white-tailed deer ($n = 14$) in the Riding Mountain National Park region, 2006–2007. Black symbols represent 2nd order selection and grey symbols represent 3rd order selection. Values are model averaged values based on all possible models run using multi-model inference (see Methods for details). Dashed line represents the intercept (no selection or avoidance).

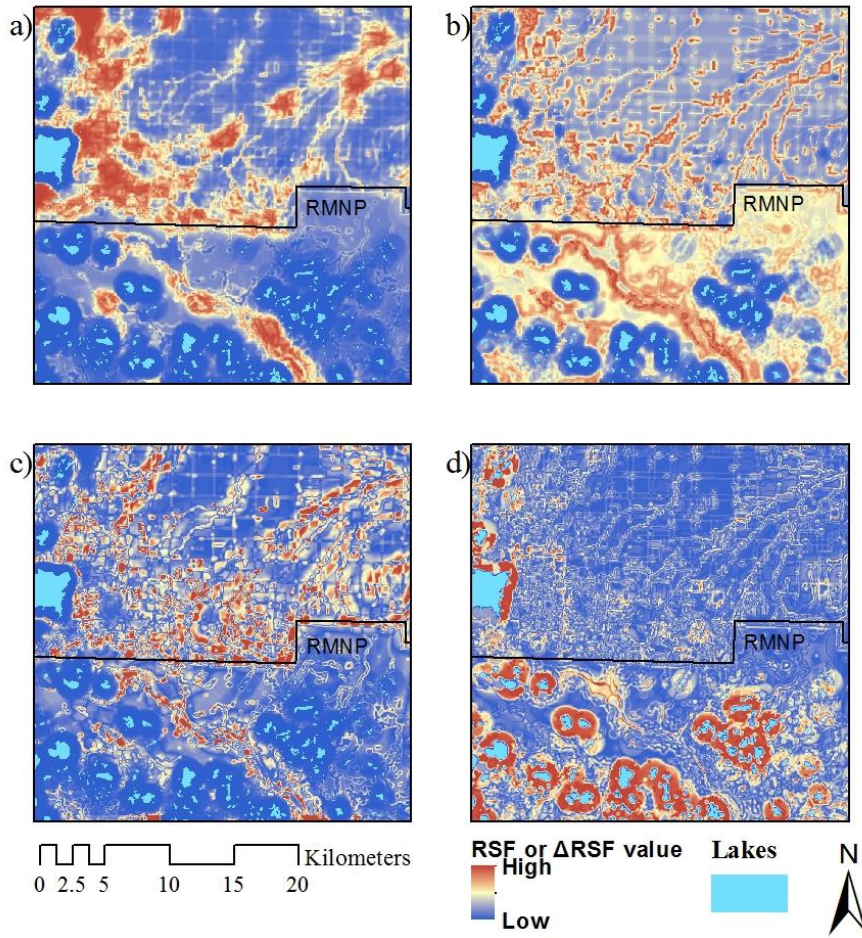


Fig. 2.4. Resource selection maps for white-tailed deer ($n = 14$ in summer, 7 in winter) in the Riding Mountain National Park region at the 2nd order of resource selection in a) winter and b) summer. Blue indicates avoidance and red indicates selection. Area below the black lines is Riding Mountain National Park (forest dominated), above is agriculture-dominated cropland. c) and d) represent a Δ RSF value defined as the absolute value of the 2nd order (c – winter, d – summer), multiple-grain RSF minus the same model computed using only the single, most explanatory grain size for all covariates. Blue values indicate similar RSF scores between models, red areas indicate differences between the models.

Chapter 3: Grain-dependent functional responses in habitat selection

3.1 Abstract

Spatial scale is a vital consideration to understanding how animals select habitat. Scale is known to affect habitat use patterns, and as such multi-scalar designs in resource selection studies have become increasingly common. Despite this, multi-scalar studies in the examination of functional response in habitat selection are rare. Studies that do examine spatial scale, either in the context of resource selection or functional response generally do so by examining patterns across selection orders (e.g., extent), and typically focus on statistical hierarchies. The perceptual range of an animal changes as a function of habitat type, suggesting that selection patterns and functional responses are both habitat- and scale-dependent. Here, I quantify the functional response of GPS collared white-tailed deer (*Odocoileus virginianus*, $n = 20$) in Riding Mountain National Park, Canada to several different habitat types. Functional responses were quantified by means of selection ratios calculated at multiple buffer sizes generated concentrically around used and available telemetry locations. I examined how functional responses changed as a function of grain size by plotting grain size against the slope of the functional response. I detected functional responses in most habitat types. Functional responses tended to converge towards 0 (use proportional to availability) at large buffer sizes, however the relationship between scale and functional response was typically non-linear and changed as a function of habitat type. I conclude that a multi-scalar approach to modelling animal functional response, informed by means of multi-grain resource selection functions, represents a key step in understanding animal resource use patterns.

3.2 Introduction

Interpretation of space-use patterns of animals is intimately linked to our understanding of animal movements through distinct habitat types, and the arrangement of those habitats will directly influence how habitat selection processes are detected and interpreted (Wiens et al. 1993). Landscapes are by their nature heterogeneous, and therefore organisms cannot always obtain an optimal combination of resources within their home range (Orians and Wittenberger 1991). As such, individuals may act as fine-grained foragers/selectors (*sensu* MacArthur and Levins 1964; where use is proportional to availability) or as coarse-grained foragers (use disproportional to availability) depending on whether the proportion of a habitat type in a home range equals the proportion of time spent in that habitat type during the diel activities of that individual. Availability is naturally variable across landscapes, and individuals can be either fine- or coarse-grained foragers depending on the relative availability of the resource in question. How availability affects the selection of habitats by animals is known as the functional response in habitat selection (Mysterud and Ims 1998).

Mysterud and Ims (1998) first adapted the classic concept of functional responses in predator-prey relationships (Holling 1959) to the study of how animals select habitat in a heterogeneous environment. A common method of quantifying functional response is by calculating a selection ratio (w_i) for each individual as a proportion of used habitat of type i divided by the available proportion of habitat i in the individual's home range (Manly et al. 2002). By plotting the log of (w_i) against proportion of habitat i available to individuals in the population, it is possible to quantify the functional response. In this instance, positive values indicate selection greater than availability and negative values indicate selection less than availability. A slope of 0 indicates no functional response (selection remaining proportional to

availability), and a steeply negative slope indicates constant use of a resource. Functional responses have been detected in ungulates (Osko et al. 2004, Godvik et al. 2009, Herfindal et al. 2009), ursids (Mauritzen et al. 2003) and birds (Gillies and St Clair 2010).

How scale affects animal resource selection is a question of fundamental importance in ecological studies (Wiens 1989, Levin 1992, Wheatley and Johnson 2009). Modifying the scale of analysis has been shown to affect resource selection patterns (Boyce et al. 2003, Anderson et al. 2005, Meyer and Thuiller 2006, Ciarniello et al. 2007, Leblond et al. 2011) and the detection of interspecific competition (Whittaker and Lindzey 2004) and sexual segregation (Bowyer et al. 1996). Spatial scale in ecology can be defined by two components, extent and grain (Hobbs 2003). Extent is the area deemed available to the animal and is typically defined by the framework established by Johnson (1980), whereas grain is typically defined as the area surrounding used and available telemetry points. Multi-scalar studies of functional responses in habitat selection are rare, and usually study the extent component of scale (Herfindal et al. 2009). To the author's knowledge, no studies have yet examined how modifying grain size affects interpretation of functional responses.

Integrating grain size into analyses of functional responses is a vital consideration in understanding the scale at which an animal perceives its environment. Animals may be selecting for patches as opposed to points (Rettie and McLoughlin 1999), making the consideration of 'landscape context variables' (*sensu* Leblond et al. 2011) vital to the study of animal space use. The relationship between scale and functional response is also likely to be dependent on habitat type and behaviour. Habitat type is known to affect vigilance behaviour in mule deer (*Odocoileus hemionus*, Altendorf et al. 2001) and red deer (*Cervus elaphus*, Jayakody et al. 2008), suggesting that habitat composition can affect the size of the perceptual range of

individuals. Animals likely have a smaller perceptual range when travelling in enclosed habitats such as forest compared to open habitats, where detection of predators becomes more important at larger spatial scales. Using buffers in the analysis of functional responses also allows for the inclusion of resources not traditionally considered in functional response studies, namely measures of habitat diversity and linear features such as roads (but see Beyer et al. 2013) and streams.

My goal was to examine functional responses at multiple grain sizes for various habitat types for white-tailed deer in Riding Mountain National Park, Manitoba, Canada and the surrounding agricultural matrix. I produced seasonal home ranges for $n = 20$ white-tailed deer (*Odocoileus virginianus*) and calculated selection ratios for each habitat type and plotted $\log(w_i)$ against availability at multiple buffer radii. I calculated the slope of the response at each scale and plotted it against grain size. I hypothesized that because individuals select habitat at different spatial scales, the functional response would change as a function of scale. Because use and availability overlap the least at smaller scales, I predicted that functional responses would be most evident at smaller scales (P_1); and that the slope of the functional response would saturate at 0 as scale increased and as use and availability converged at the largest scales (P_2). I also predicted that the shape of the function generated when plotting functional response slope against scale would vary based on the resource being examined (P_3).

3.3 Methods

3.3.1 STUDY AREA

The study area was located in southwest Manitoba, Canada. The area contains two distinct habitats: the forest-dominated area within Riding Mountain National Park (RMNP) and the surrounding agricultural matrix. RMNP is a 2,974 km² protected area that consists of eastern deciduous forest, northern boreal forest and rough fescue grasslands with areas of wetland (Rowe 1972, Caners and Kenkel 2003). Higher elevations in the park are dominated by spruce (*Picea* spp.), pine (*Pinus banksiana*) and aspen (*Populus tremuloides*). The area surrounding the park is intensively managed for the production of annual cereal and oilseed crops, perennial forage crops and as cattle pasture (Brook 2010), interspersed with deciduous forest, wetland and grassland.

The area is populated by a large diversity of wildlife species. During the study period, it was estimated that there were approximately 2700 elk (*Cervus canadensis*), 2500 moose (*Alces alces*) and a large population of white-tailed deer (Brook and McLachlan 2006). Predators in the area include wolves (*Canis lupus*), black bears (*Ursus americanus*), lynx (*Lynx canadensis*) and coyotes (*Canis latrans*).

3.3.2 DATA COLLECTION AND HABITAT VARIABLES

White-tailed deer ($n = 18$ female and 2 male) were captured via a net gun fired from a helicopter (Cattet et al. 2004) in February 2006 and fitted with GPS tracking collars. Collars were active for one year and recorded locations at 2 – 4 hour intervals. Individuals were captured in the agricultural area north of RMNP and in the north of the park but were free to enter or exit the park at any point along the boundary. A total of 21,364 locations were collected, with a mean of 422 (SE = 45.5) locations per animal per season.

I created seasonal 95% minimum convex polygon (MCP) home ranges (Osko et al. 2004, van Beest et al. 2010) for each deer ($n = 56$ deer seasons). MCPs were used as a simple method to delineate used and available resources (Godvik et al. 2009, Herfindal et al. 2009). I delineated seasons based on periods of increased movement rates of white-tailed deer presented in van Beest et al. (2013). I buffered home ranges by 327 m (the mean distance travelled between successive GPS fixes) to better reflect the area available to individuals. Within each individual's buffered home range I generated random points equal to the number of GPS fixes. Telemetry points located in lakes were removed ($n = 15$) and lakes were excluded when generating random points, since lakes were not deemed habitat useable by deer.

I quantified several environmental covariates at the resolution of the data and in concentric buffers around used and available points at radii of 75, 150, 327, 500, 750 and 1000 m using ArcMap (ArcGIS 10, ESRI Redlands, California, USA) and Geospatial Modelling Environment (Beyer 2012). I assessed land cover using 30 m resolution Landsat 5 satellite imagery (Geobase: <http://www.geobase.ca>). Field validation was performed in 2011 and showed that 84% of validated points were accurate, with the majority of misclassified points being due to changes in agricultural cropland (Dugal 2012). Within each buffer I calculated the proportion of forest, annual cropland, perennial cropland, grassland and wetland as well as density of streams and unpaved roads ($m \times ha^{-1}$). I used Simpson's Diversity Index as a measure of landscape heterogeneity, because it was most descriptive of white-tailed deer habitat use in RSF modelling for this population.

3.3.3 QUANTIFYING FUNCTIONAL RESPONSE

I used log transformed selection ratios to measure functional response. For each individual, I calculated the mean of each habitat type in used and available buffers within each seasonal home range and calculated selection ratios for each season/individual by taking the log of w_i , where w_i equals:

$$w_i = o_i / \pi_i \quad (3.1)$$

Here, o_i represents the mean value of covariate i in used locations/buffers. This represents a simple mean for linear features/Simpson's Diversity, a proportion of locations for observations at the resolution of the data (e.g., no buffers, Manly et al.'s [2002] original definition), and a mean proportion of habitat i within buffers for scales using buffers. I added 0.0000001 to used points to allow calculation of an odds ratio when use = 0. Linear features and diversity were not quantified at the resolution of the data (e.g., only quantified in analyses using buffers). π_i was calculated in the same way using available points/buffers. Seasonal home ranges with zero availability for a resource type were excluded in analyses on that resource type. At each grain of analysis, I plotted $\log(w_i)$ of selection against proportion of habitat available to determine the functional response, where a slope of zero indicates no functional response (use remains proportional to availability as availability changes). To determine the effect of changing grain of analysis on functional response, I estimated the slope and standard error of the functional responses at each grain of analysis and plotted slope against scale for each habitat type.

3.4 Results

I detected functional responses across most habitat types examined. As habitat availability within individual home ranges increased, selection ratios either increased or decreased, depending on scale and habitat type.

I found a significant interaction between grain size and functional response. Of the eight habitat types examined, five had a 95% confidence interval (CI) for the slope of the functional response that did not overlap the 95% CI of the slope of the response at at least one other grain size, suggesting that grain size had an important effect on functional responses. Functional responses were usually most evident at small and intermediate scales, however smaller scales were also associated with larger standard errors (Fig. 3.1).

Each habitat type displayed its own type of functional response, and showed a unique interaction with grain size (Fig. 3.2). Forest had a strongly negative functional response at small buffer sizes, suggesting use of forests did not increase at the same rate as availability within the home range. As grain size increased, the slope of the functional response also increased towards zero. Wetland and stream density had positive slopes at small grain sizes, suggesting individuals increased their relative use of these habitats as availability increased. As with forest, the functional response appeared to saturate at zero with increasing grain size (Table 3.1). For some habitat types, the functional response was strongest at the smallest grain examined (forest, wetland, stream density), however in others the strongest functional response was found at intermediate grains.

Certain covariates (both types of cropland, road density and grassland) appeared to have a positive slope at some scales and a negative slope in others, suggesting different types of

functional responses may be detected at different scales. Likewise, many covariates displayed a functional response at one scale yet failed to display one at others, suggesting our detection of functional response is indeed both scale- and habitat-dependent.

3.5 Discussion

I found a significant effect of grain size on the interpretation of white-tailed deer functional response. Each habitat type displayed a unique relationship between functional response and grain size (in support of P_3), with all habitat types displaying a tendency to saturate at 0, supporting P_2 . The strongest functional response was either detected at the smallest grain or at intermediate grains—providing moderate support for P_1 that the smallest grains would result in a larger functional response. These results demonstrate that how ecologists interpret functional response is dependent on the scale at which it is examined.

Animal habitat selection is based on tradeoffs, with individuals typically having to balance the acquisition of optimal forage with the risk of predation (Sih 1980). In ungulates, this involves balancing foraging bouts in more productive open habitats where predation risk is higher against ruminating and resting in covered forest habitats (Mysterud et al. 1999). As such, as availability of profitable foraging (open) habitats increases, we should see an increase in their use, however due to time budgets, we would not expect a constant increase. Therefore, the functional response is expected to be between constant and proportional use, termed the ‘real world trade-off hypothesis’ by Godvik et al. (2009). My results suggest that changing the scale at which observations are made affects the interpretation of this trade-off, and as such underscore the importance of examining scale in functional response studies.

Despite the acceptance of the importance of scalar processes to the examination of animal habitat selection (Wiens 1989, Levin 1992), they have rarely been examined in the context of functional responses. Herfindal et al. (2009) found that home range size was an important factor in functional response at both the home range- and landscape-level of selection; however, they did not consider how the relative abundance of different habitat types affects functional response. Functional response can vary across selection orders (Herfindal et al 2009), therefore varying grain size for different resources may encompass different levels of selection on continua of scales. Habitat selection, and as a result functional response, is influenced not only by the composition of habitats but also by their configuration (Stubblefield et al. 2006, Radford and Bennett 2007). As such, the inclusion of buffers in functional response studies is important for two reasons. Firstly, it incorporates patch size into the analysis, which is an important factor in habitat selection studies (Rettie and McLoughlin 1999). Secondly, it allows for the inclusion of habitat types surrounding an individual location, which may have an impact on resource selection patterns. For example, an individual may choose to forage in open habitats that are near closed habitats as potential refuge from predators.

In both annual cropland and in grassland habitats, the functional response shifted from being positive without the use of buffers to a negative response with buffers. This could reflect the use of small patches or edge habitats, as well as be a function of the relative configuration of these habitats across the landscape, since the buffers must be encompassing other habitat types at this scale to result in a change in the functional response. It is therefore likely that the level of fragmentation of the landscape and the relative size of habitat patches is a vital determinant of how scale interacts with functional response.

White-tailed deer displayed a positive functional response to roads that was highest at intermediate (750 m) scales, suggesting that as the density of unpaved roads increased in their seasonal home ranges, white-tailed deer increased their use of areas within a 750 m radius of roads. Moose have been shown to select for roads at intermediate scales (Rempel et al. 1997) while avoiding them at small scales (Dussault et al. 2007). By contrast, elk (*Cervus canadensis*) have been shown to avoid roads at the landscape scale and select for roads at smaller scales due to their association with edge habitat (reviewed by Anderson et al. 2005). Beyer et al. (2013) found a functional response to road crossings in moose. My results show that there is an interaction between scale of observation and functional response in how ungulates select habitat surrounding roads.

The interaction between buffer size and functional response varied by habitat type, indicating a change in how animals respond to scale across habitats. To navigate across landscapes, animals use cues from the landscape (either via environmental gradients or navigational beacons; Fagan et al. 2013) and by means of spatial memory. Animal behaviour varies as a function of habitat (Altendorf et al. 2001, Jayakody et al. 2008); therefore how an animal travels through a landscape will be directly affected by the composition and configuration of that habitat. An animal's perceptual range is not fixed, but varies across habitat types (Olden et al. 2004), influencing the scale at which habitat selection decisions are made and subsequently the spatial scale of the functional response.

I have shown that the functional response of white-tailed deer habitat selection is contingent upon the spatial scale of investigation. Is there a “best” scale at which to make conclusions for functional responses? Animals face different pressures at different scales, often simultaneously. Habitat management likewise occurs on many spatial scales, with the

establishment of protected areas or policies on hunting quotas occurring at broad spatial scales to fencing on individual farms which occur on small scales. As such, prescribing an ideal scale for any analysis (or indeed, even for a single resource), may be impossible. By contrast, functional responses are likely to be most ecologically relevant at scales at which selection is known to be highest. Future studies could incorporate a multi-grain resource selection approach to determine what grain sizes are most relevant for each habitat type and incorporate them into functional response studies. In conclusion, multi-scalar approaches to the quantification of animal functional responses represent an important step forward in our interpretation of animal habitat selection.

Tables and Figures

Table 3.1: Slope of $\log(w_i)$ functional responses and standard errors of white-tailed deer across four seasons ($n = 56$ deer seasons) to different resource types in Riding Mountain National Park, 2006–2007.

Resource↓	Scale (m)→	30*	75	150	327	500	750	1000
Forest	slope	−1.88	−1.65	−1.40	−0.88	−0.58	−0.37	−0.30
	S.E.	0.22	0.23	0.24	0.22	0.18	0.13	0.11
Annual cropland	slope	0.59	−1.18	−0.95	−0.59	−0.35	−1.00	−0.56
	S.E.	1.71	0.48	0.35	0.25	0.21	0.44	0.45
Perennial cropland	slope	3.68	0.54	−1.59	5.09	6.26	4.32	2.20
	S.E.	16.10	13.48	11.38	8.80	6.12	5.09	3.30
Wetland	slope	30.77	13.64	11.42	2.90	3.84	2.19	1.76
	S.E.	9.55	7.77	6.53	1.52	2.33	1.46	0.85
Grassland	slope	1.70	−1.88	−2.38	−1.75	−1.27	−0.56	−0.45
	S.E.	2.82	0.97	0.92	0.69	0.70	1.18	1.22
Stream density	slope	NA	0.43	0.25	0.05	0.02	0.03	0.10
	S.E.	NA	0.24	0.13	0.04	0.03	0.02	0.04
Road density	slope	NA	0.06	0.00	0.18	0.22	0.34	−0.11
	S.E.	NA	0.04	0.04	0.09	0.09	0.13	0.09
Simpson's Diversity	slope	NA	0.00	−0.17	−0.12	−0.11	−0.15	−0.20
	S.E.	NA	1.23	0.57	0.37	0.28	0.20	0.15

* Plotted at the resolution of habitat data (no buffers used). NA for linear features and diversity.

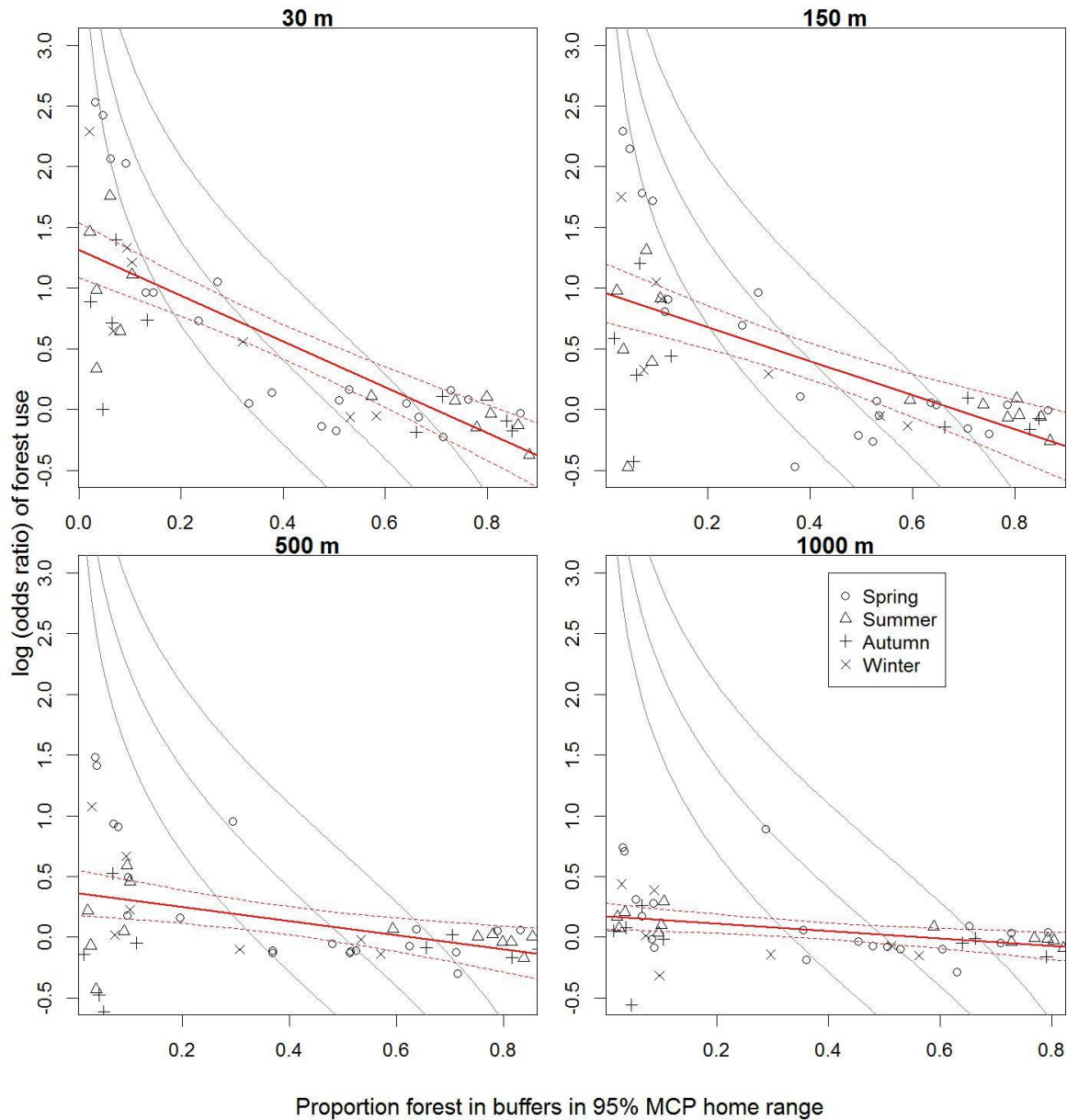


Figure 3.1: Functional response of white-tailed deer across four seasons ($n = 56$ deer seasons) to forest habitat at four grains of analysis in Riding Mountain National Park, 2006–2007. The red line is the slope of the functional response, with a 95% confidence envelope represented by a dashed line. A slope of zero would represent proportional use, and the grey lines indicate constant use at a proportion of 0.25, 0.50 and 0.75.

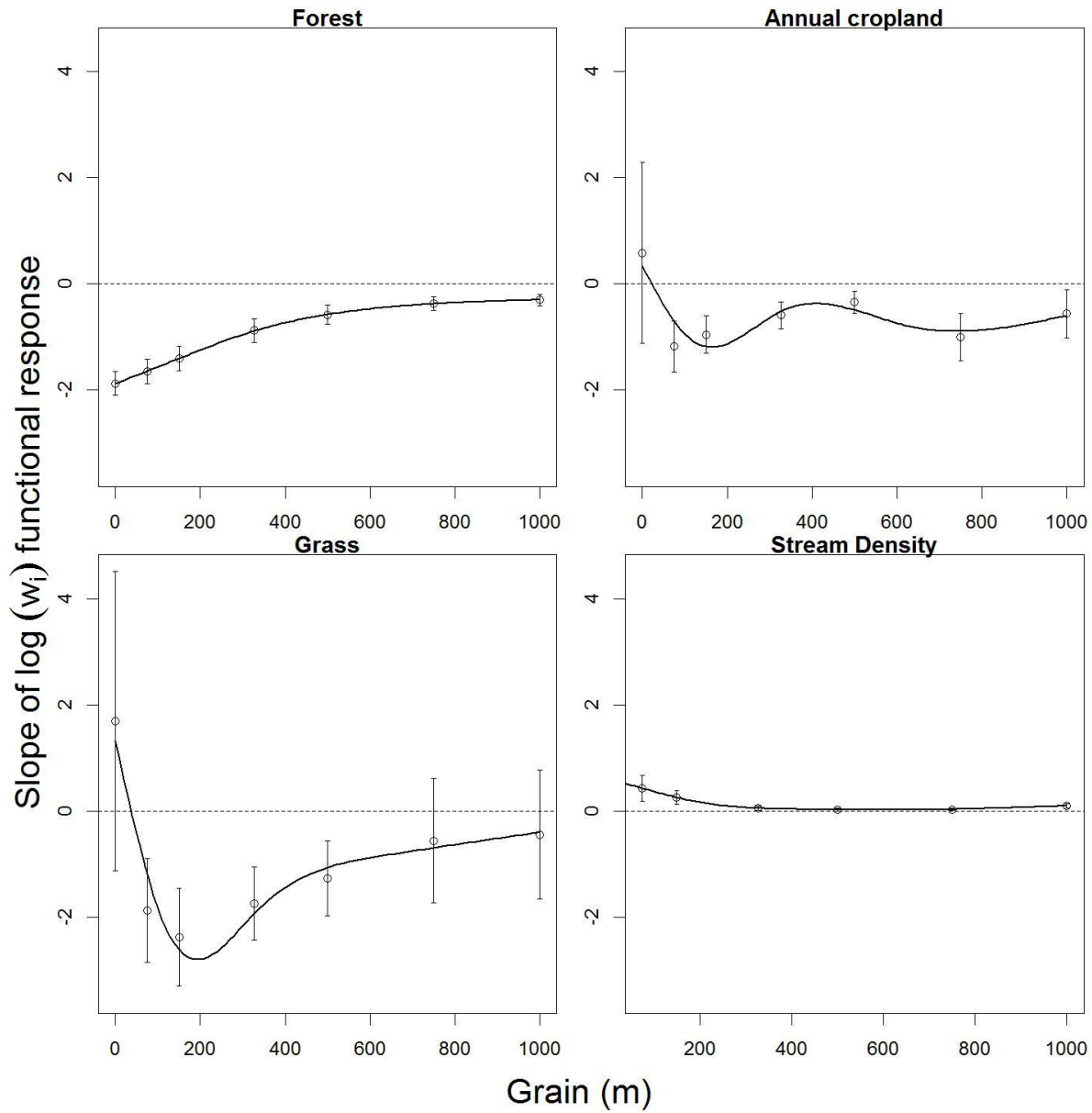


Figure 3.2: Slope and 95% confidence intervals for functional responses across several grains of analysis for white-tailed deer ($n = 20$) in Riding Mountain National Park, 2006–2007. Dashed line indicates a slope of zero (proportional use at that grain). Curves were fit using generalized additive modeling.

Chapter 4: Discussion

4.1 Thesis overview

I examined the impact of scale, most notably the effect of the inclusion of buffers, on resource selection in white-tailed deer. A total of $n = 20$ GPS collared individuals were captured in the agricultural region surrounding Riding Mountain National Park, Manitoba, Canada. I generated concentric buffers of varying radii around used and randomly generated available points at both the home-range- and landscape-scale. Using multi-model inference techniques, information theory (AIC) and selection ratios I determined how resource selection and functional response patterns changed as a function of grain.

My objectives were:

- (1) To quantify white-tailed deer resource selection patterns across multiple grains at both the within-home-range- and landscape-scale, examining how scale and habitat type interact in informing habitat selection patterns.
- (2) To develop a method of evaluating and comparing covariates measured at multiple grains to inform the construction of multi-grain resource selection functions (MRSFs).
- (3) To examine how changing buffer sizes affects the interpretation of white-tailed deer functional response by means of selection ratios.

My conclusions were:

- (1) That multi-grain resource selection functions result in lower AIC scores and better cross-validation scores than models computed at only a single grain of analysis.

- (2) That the scale of animal behaviour and movement is a habitat-dependent process based on an animal's perceptual range and spatial memory.
- (3) That multi-grain resource selection functions represent an important step forward in how ecologists model animal habitat selection.
- (4) That the functional response is a habitat- and grain-dependent process and that studies of functional response should include the use of multiple grains, informed by means of MRSFs.

4.2 Scale in wildlife research

Habitats by their nature are heterogeneous, and as a result the home ranges of animals rarely contain an ideal proportion of habitat resources. Understanding how animals use landscapes and habitats available to them has been a fundamental question in ecology for decades (MacArthur and Pianka 1966, Rosenzweig 1981). More recently, the importance of the scale of analysis in ecological studies has become evident (Turner et al. 1989, Schneider 2001). While multi-scalar studies have become common (i.e., Rettie and Messier 2000, Kie et al. 2002), studies tend to focus on the extent component of scale while ignoring the grain component. My results show that grain is an important consideration in the study of animal habitat selection, and provide a methodological framework from which to evaluate habitat use across multiple grains.

I found that multi-grain resource selection functions had lower AIC values and better k -fold cross-validation scores than models computed at a single grain of analysis. I evaluated my models by comparing model-averaged β coefficient values and sum of Akaike weights (w_i) across grains. I also used a novel method to evaluate variable importance across scales where the AIC value of a global model was compared against a quasi-global model in which the focal variable was dropped at each grain. My results show that white-tailed deer habitat selection is a

grain- and habitat-dependent process, as selection changed across scales for almost all habitat types.

The perceptual range experienced by an animal while navigating a landscape is an important consideration in studies of animal movement; however, few studies incorporate perceptual range when modelling animal distributions. My results illustrate the importance of perceptual range across habitat types in animal habitat selection and outline a method for quantifying it in the context of resource selection functions. I conclude that spatial memory plays an important role in the interpretation of MRSFs, as animals use landscape cues to navigate through landscapes. The incorporation of grain also made possible the quantification of selection for habitat diversity, as measured by Simpson's Diversity Index, which proved to be important at all spatial scales.

I also found an interactive effect between functional response in habitat selection and grain size, a previously unexamined relationship. I quantified functional response using selection ratios computed at multiple grains and plotted grain of analysis versus the slope of the functional response. I found that the grain at which resources are quantified had an important effect on the detection of functional response. The examination of multiple grains in the study of functional response successfully incorporated patch size and surrounding vegetation types to elucidate grain-dependent changes in functional responses.

4.3 Management implications

Human-wildlife conflict is a major concern in the RMNP region. White-tailed deer are considered a nuisance species to agriculture, with many crops being damaged by white-tailed deer. The risk of disease transmission between wild and domestic cervids is a concern. Bovine

tuberculosis (TB; *Mycobacterium bovis*; Brook and McLachlan 2006) is a problem in the RMNP region, and the risk of chronic wasting disease (CWD) being introduced to the province from infected individuals in Saskatchewan remains an ever-present concern (Williams et al. 2002, Salman 2003). TB can be transferred between wildlife and domestic herds via direct transmission via sneezing and coughing (Garnett et al. 2002), or through indirect means such as contact with shared grain or pasture or through contact with contaminated saliva, urine or faeces (Hutchings and Harris 1997). Herds found to have an individual infected with TB are depopulated at great expense to producers and governments (Brook and McLachlan 2009). CWD transmission can occur through direct contact or from exposure to infected saliva or blood (Mathiason et al, 2006) and herds with an infected individual also face depopulation (Salman 2003).

The spectre of disease transmission between individuals, sub-populations or even species confounds how managers must manage these species and the landscapes upon which they live. Conventional conservation wisdom suggests that functionally connected wildlife habitat should be a positive outcome for species management, increasing population range and gene flow between sub-populations (Beier and Noss, 1998). However, greater movement of individuals will result in increased disease transmission (Hess 1994). Areas of highly suitable habitat are likely to have an increased density of individuals, which has shown to increase the rate of direct contact between individuals (Vander Wal et al. 2014) in ungulates, increasing the risk of pathogen transmission.

My results provide insight into how landscapes can be managed in order to control white-tailed deer populations. White-tailed deer were found to prefer areas with a diversity of landscapes at intermediate (~300 – 500 m) grains with a high diversity of habitat types. Such a landscape would promote white-tailed deer movement; however, where management is

concerned with the spread of disease or crop damage, a more homogeneous agricultural landscape would be preferred. The identification of areas of overlap between white-tailed deer and elk habitat could provide managers with invaluable information to help mitigate interspecific disease transmission. Future research should look to comparing RSFs computed for the two species as a means to identify such areas of concern.

Decisions related to wildlife management are made at multiple spatial scales, from decisions on establishment of protected areas and hunting zones at the broadest scales to stand-level management and the use of barrier fencing at finer scales (Ciarniello et al. 2007, Brook 2010). This is not always an easy task, as it makes the prescription of “ideal” habitat for a given species nearly impossible, as the answer is almost invariably scale-dependent—the optimal set of landscape variables for establishing a home range are often not the same as those that will predict use within the home-range. The multi-grain resource selection function, as outlined here, represents a broadly-applicable tool that could provide wildlife managers with a unique method of analyzing resource use patterns across scales in order to make informed decisions on land use planning.

4.4 Study limitations and future directions

My study has shown how MRSFs can be an improvement over conventional RSFs, however the new method does have some limitations, some of which are inherent to all RSF studies. Autocorrelation between points may have introduced some bias to the results. A longer-term dataset spanning multiple years would have provided a more complete view of seasonal resource selection, which may have been more influenced by weather given the (relatively) short temporal scale of this study. The dataset used in this study was heavily female-biased, making

the separation of sex effects difficult. A larger diversity of grain sizes, as well as an analysis of interaction terms, may provide more accurate results, however complications due to correlation between covariates and difficulties in achieving convergence in the models would need to be overcome in order to make this feasible.

4.5 Conclusion

The use of multiple grains to model animal habitat selection has remained underappreciated in the ecological literature. Here I demonstrated that more attention should be given to multi-grain processes and outline a method by which the effect of grain can be quantified in both a functional response and resource selection context. The multi-grain resource selection function I have introduced here offers a step forward in our understanding of animal habitat selection. By modelling each habitat type at a different grain, I have shown how perceptual range and spatial memory may play a habitat-dependent role in determining how scale interacts with resource selection.

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Appendix A: Supplementary figures

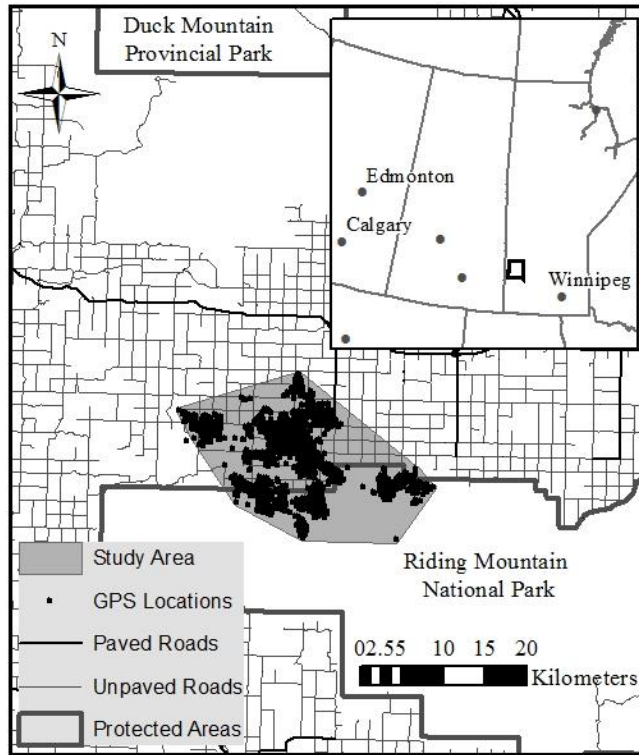


Fig. A1 Riding Mountain National Park and surrounding agricultural region. Shaded area represents the study area with points representing locations of collared white-tailed deer, 2006–2007.

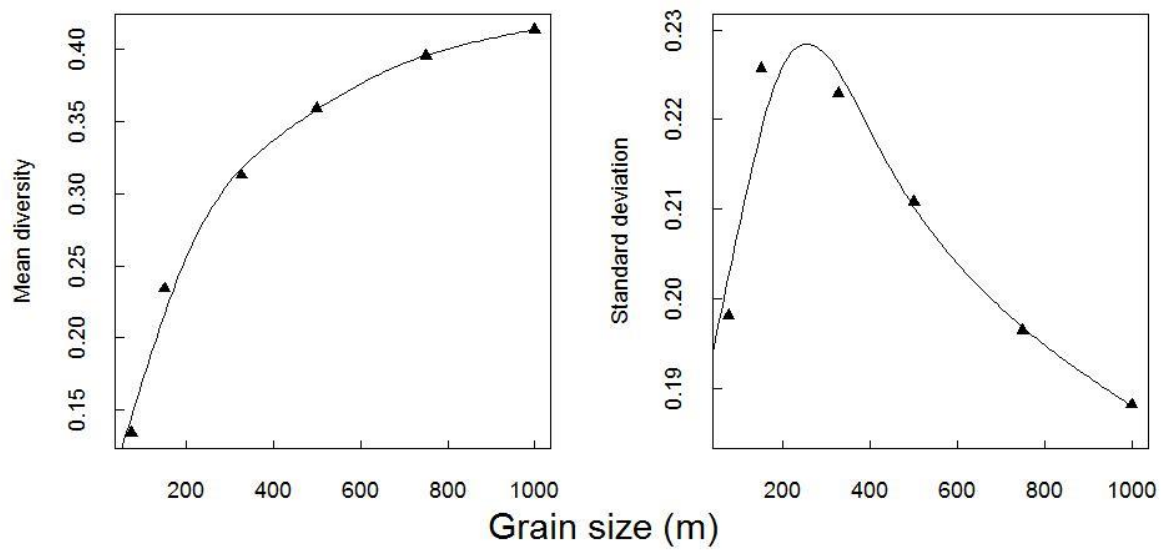


Fig. A2 Variability of habitat heterogeneity across grain sizes of random points in the Riding Mountain National Park region.